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Morphometric study of the cochlea of the rabbit (*Oryctulagus cuniculus*)[1]

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A detailed morphometric study of the cochleae in four rabbits (*Oryctulagus cuniculus*) was made from graphic reconstructions of serial sections. Morphometric changes studied along the length of the cochlea were (*i*) the cross-sectional areas of the scalae vestibuli, tympani, and media, (*ii*) the width of the basilar membrane, (*iii*) the cross-sectional area and thickness of the basilar membrane, and (*iv*) the density of the bipolar ganglion cells innervating the organ of Corti. Changes in the cross-sectional areas of the scalae tympani and vestibuli were similar, both decrease from the cochlear base to 1.2 mm, increase to maximum values of 1.4 mm^2 at 3.0 mm, and decrease to 0.4 mm^2 at 4.3 mm. The cross-sectional area of the scala media remained unchanged. Three distinct morphometric changes were observed in the width and cross-sectional area of the basilar membrane. Firstly, there is a steep increase from the basal end to 3.2 mm, secondly a gradual increase from 3.2 to 8.5 mm, and thirdly, the greatest values occurred between 8.5 and 9.1 mm. The average number of bipolar ganglion cells estimated within the spiral ganglion was 26 700. The density of ganglion cells decreased from the base to 1.9 mm and then increased to its greatest density of 2800 cells/mm^2 between 8.5 and 10.5 mm. The location of maximum density coincided with the location of the basilar membrane where the stiffness gradient was relatively uniform.

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La reconstitution graphique de séries de coupes a permis d'étudier à fond la morphométrie du limaçon chez quatre lapins (*Oryctulagus cuniculus*). Les variations morphométriques étudiées le long de l'osselet sont (*i*) la surface des coupes transversales des rampes vestibulaire, tympanique et médiane, (*ii*) la largeur de la membrane basilaire, (*iii*) la surface de la coupe transversale de la membrane basilaire et son épaisseur et (*iv*) la densité des cellules ganglionnaires bipolaires associées à l'organe de Corti. Les variations dans la surface de la coupe transversale des rampes tympanique et vestibulaire sont semblables: les deux diminuent de la base du limaçon jusqu'à 1,2 mm, augmentent ensuite jusqu'à des valeurs maximales de 1,4 mm^2 à 3,0 mm, pour diminuer de nouveau jusqu'à 0,4 mm^2 à 4,3 mm. La surface de la coupe transversale de la rampe médiane ne varie pas. Il y a trois changements morphométriques dans la largeur et dans la surface de la coupe transversale de la membrane basilaire. D'abord, il y a une augmentation brusque depuis la base jusqu'à 3,2 mm, puis une augmentation graduelle de 3,2 à 8,5 mm, enfin une augmentation jusqu'aux valeurs maximales entre 8,5 et 9,1 mm. Le nombre moyen de cellules ganglionnaires bipolaires a été estimé à 26 700 dans le ganglion spiralé. La densité des cellules ganglionnaires diminue de la base jusqu'à 1,9 mm, puis augmente pour atteindre son maximum entre 8,5 et 10,5 mm. La densité maximale de cellules coïncide avec le point de la membrane basilaire où le gradient de rigidité est à peu près uniforme.

[Traduit par le journal]

Recent studies of the mammalian cochlea have attempted to correlate psychoacoustic and neuroanatomic data with pertinent cochlear morphometric dimensions (Bruns 1976*a*, 1976*b*; Ehret and Frankenreiter 1977; Ramprashad *et al.* 1978; Ramprashad *et al.* 1979). Morphometric studies of the microchiropteran cochlea suggested that the frequencies used for echolocation coincided with a region of the basilar membrane in which morphological discontinuities occur (Bruns 1976*a*, 1976*b*; Ramprashad *et al.* 1979). Furthermore, Ehret and Frankenreiter (1977) have indicated that although the house mouse (*Mus musculus*) is maximally sensitive to 15 kHz, the frequency of 50 kHz also occurs within a region of morphological discontinuity in the basilar membrane. Moreover, Ramprashad *et al.* (1984) have shown that in the two-toed sloth (*Choloepus* sp.), the frequency of greatest sensitivity (1.0–1.5 kHz) is also coincident with a region of morphological discontinuity in the basilar membrane. It appears, therefore, that when correlated with appropriate morphometric parameters, psychoacoustic data may provide a meaningful picture of frequency transduction along the basilar membrane. The present study attempts to ascertain if a correlation of this kind is present in the rabbit.

Martin *et al.* (1980) have determined psychoacoustic data for pigmented and albino rabbits using the classical conditioned nictitating membrane response. They showed that the frequency range of hearing in the rabbit is 0.3–32.0 kHz, with the maximally sensitive frequencies occurring between 8 and 16 kHz. Martin *et al.* (1980) also noted that the rabbit's audiogram corresponds very closely to the hypothetical average mammalian audiogram described by Masterton *et al.* (1969), so that it would be useful to correlate pertinent morphometric parameters and neuroanatomical data with the available psychoacoustic data in this species.

Materials and methods

Four male, adult, common pigmented domestic rabbits (*Oryctulagus cuniculus*) with an average body mass of 3.7 kg were given an overdose of Nembutal®; the animals were decapitated and the heads were skinned and immersed in Heidenhain–Susa fixative and processed according to the procedures of Igarashi (1966) and Schuknecht (1953). The process consists of a 6- to 8-week period of decalcification and dehydration and a 4-month embedding period in celloidin. After hardening of the celloidin, each head was serially sectioned with a sliding microtome at 20 μm. Two heads were sectioned horizontally,

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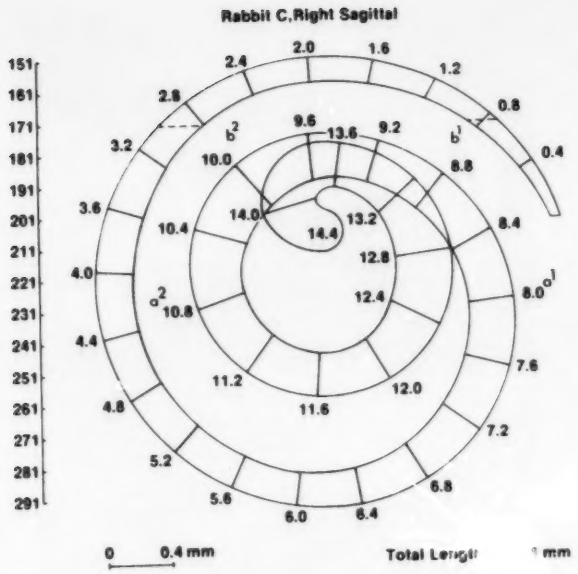

FIG. 1. Graphic representation of the width of the basilar membrane of one of the rabbits (right ear, rabbit C, from sagittal sections); measured length, 14.4 mm. The dotted lines, b^1 and b^2, are the measured widths on a particular slide from a series of serial sections whose slide numbers are shown to the left of the figure. The radial lines, a^1 and a^2, are the radial lines which gives the approximate widths at known distances along the length of the cochlea, in particular in the tangential sections. The numbers along the coil represent the distance (millimetres) from the basal end of the cochlea. Note that the cochlea is approximately a 2.5-turn spiral.

one frontally, and the fourth sagitally. Initially, every fifth section was mounted (cf. Guild 1921; Igarashi 1966) and stained in Harris' ammoniated haematoxylin and eosin. Additional sections were stained and mounted to obtain further morphometric data as indicated later. The method employed produces a tissue shrinkage artifact of between 9 and 10% (Schuknecht 1974; Igarashi *et al.* 1981).

The change in width of the basilar membrane was determined by first making a graphic reconstruction of the coils of each cochlea by using every fifth slide according to the methods of Guild (1921) and Schuknecht (1953). The delimitations used to measure the width of the basilar membrane were from the medial base of the inner pillar cell to the spiral ligament junction (Fig. 4). The measured widths of the basilar membrane were then projected as horizontal lines on the graphic reconstruction (see lines b^1 and b^2 in Fig. 1) from every second slide in the series. The ends of these lines were then interconnected to represent a graphic reconstruction of the basilar membrane (Fig. 1.) (Wever 1938; Wever *et al.* 1971). The approximate width of the basilar membrane at any given point can be determined from this graphic reconstruction by drawing a radial line through the centre of curvature for the half coil of the cochlea (e.g., see lines a^1 and a^2 in Fig. 1). In this way the change in width of the basilar membrane can be correlated with distance along the length of the cochlea and the value of the approximate width of the basilar membrane could be determined from the tangential series. A graphic plot of width versus distance was made for each cochlea from the horizontal and sagittal series (Fig. 3). From each graphic plot the degree of obliquity of the plane of sectioning at a particular location can be determined by the ratio of approximate width to measured width of the basilar membrane. This correction factor ratio was used to correct all morphometric data measured at that point along the cochlea (Weaver 1938; Wever *et al.* 1971).

A camera lucida was used to draw on graph paper the outline of the cut surfaces of the pars pectinata, pars tecta, the sum of both these

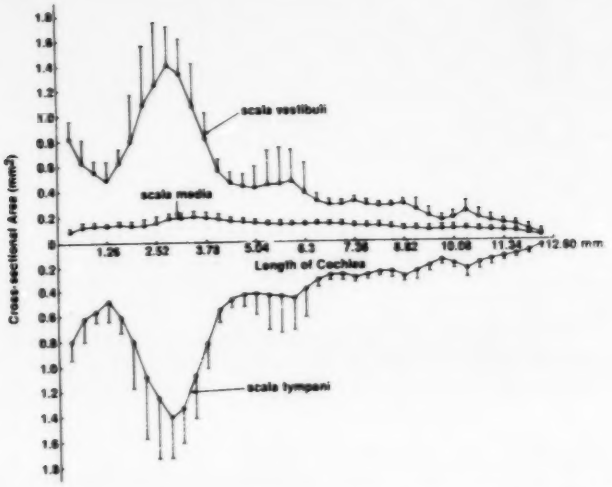

FIG. 2. Graph depicting the changes in the cross-sectional areas of the scalae vestibuli, tympani, and media along the length of the cochlea. The dots and vertical bars represent the mean values and standard deviations, respectively. Note (*i*) the small change in the cross-sectional area of the scala media along the entire length of the cochlea and (*ii*) the similarity in the curves for the areas of the scalae vestibuli and tympani (e.g., similar maximum values coincide at approximately 3.0 mm from the basal end of the cochlea).

areas (to represent the cross-sectional areas of the basilar membrane), the scalae media, tympani and vestibuli, and the spiral ganglion (Ramprashad *et al.* 1979). The procedure was as follows. The cross-sectional areas of the pars pectinata, pars tecta, and the sum of both areas and the cross-sectional areas of Rosenthal's canal and the scalae media, tympani, and vestibuli were measured with a Numonics optical planimeter linked to a Science Assessories Corporation (S.A.C.) sonic digitizer and a microcomputer. The basic program permitted the recording of four measurements per trace, the average of the four measurements, and the conversion of that average into square millimetres. This value was then multiplied by the correction factor determined as above for that specific location along the coil of the cochlea. This procedure was followed with every second slide of a particular series. A graphic plot of the measured cross-sectional area versus distance along the length of the cochlea was made for each ear. In this way values at tangential sections could be extrapolated from each graph. Enumeration of the bipolar ganglion cells within the cross-sectional area of Rosenthal's canal was determined under high-power, light-microscopic magnification with the aid of a 100× 1-mm graticule in a 10× eyepiece. A graphic projection of the coils of Rosenthal's canal was made by measuring the distances from the edges of the canal of the spiral ganglion to the medial base of the inner pillar cells. Using the initial trace of the coil of the cochlea as determined previously, these distances were represented as horizontal lines; the lines were then interconnected so that the outline and thickness of the spiral ganglion could be represented throughout its spiral course. From this graphic reconstruction it is possible to correlate a specific cross-sectional area of Rosenthal's canal at an approximate position of the length of the cochlea (cf. Ramprashad 1976; Ramprashad *et al.* 1978; Ramprashad *et al.* 1979). The total number of ganglion cells for each cochlea was determined from each graphic reconstruction. Corrections for "split cell error" were made using the Abercrombie formula (Konigsmark 1970). The density of bipolar ganglion cells (i.e., the number of bipolar cells per unit cross-sectional area for each cut surface of the spiral ganglion) was determined by dividing the number of cells counted by the cross-sectional area at that location. A graphic plot of density versus cochlear length was made for each cochlea. In this way the density of ganglion cells in a tangential section could be extrapolated from the graph (cf. Ramprashad 1976;

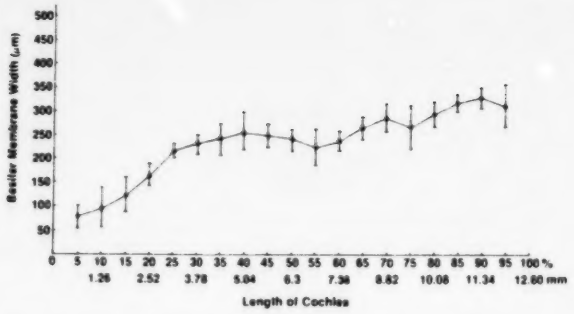

FIG. 3. An illustration of the gradual change in width of the basilar membrane along the length of the cochlea. The dots and vertical bars represent the mean values and standard deviations, respectively.

Ramprashad *et al.* 1978; Ramprashad *et al.* 1979).

Since the length of the cochlea was different for each animal (range, 11.8–14.4 mm; mean length, 12.6 mm), distances along each length were converted into percentages of the total length (Bohne and Carr 1979). From the graph of each ear, fixed percentage distances along the length of the basilar membrane were selected and the values were averaged for each of the parameters studied. These averaged values were then plotted against the fixed percentage lengths along the basilar membrane to construct a representative graph for each parameter measured in the rabbit's cochlea. Percentage distances were then converted into representative distances (millimetres) using the mean length of the cochlea.

Results

Change in cross-sectional area of the scalae

Figure 2 illustrates the changes in the mean cross-sectional areas of the scalae vestibuli, media, and tympani along the length of the rabbit cochlea. The cross-sectional areas of the scalae vestibuli and tympani decrease rapidly from the oval and round windows to about 0.5 mm^2 at a distance about 1.2 mm from the basal end of the cochlea; they then increase to maximum areas of 1.4 mm^2 at 3.0 mm. There are sharp decreases in their areas to about 0.4 mm^2 at 4.3 mm along the coil and then a gradual decrease to the apex. The cross-sectional area of the helicotrema was estimated at 0.1 mm^2. The mean cross-sectional area of the scala media remains relatively unchanged throughout the length of the cochlea.

Change in width of the basilar membrane

The rabbit's cochlea consists of a 2.5-turn coil (Fig. 1).

Figure 3 depicts an overall gradual change in the width of the basilar membrane from 79 μm at the base to a maximum width of 325 μm at the apex of the cochlea. This gradual change in width from the base to the middle and apical coil is evident in Fig. 4A–4C.

Change in cross-sectional area of the basilar membrane

The mammalian basilar membrane is divided into two parts: the pars tecta and the pars pectinata (Fig. 4). Figure 5 illustrates the change in the cross-sectional area of the basilar membrane, as well as the changes in the pars tecta and the pars pectinata. It also shows that the cross-sectional areas of both the pars tecta and the pars pectinata increase gradually for most of the length of the cochlea, attaining maxima between 8.5 and 9.1 mm from the basal end. The change in the cross-sectional area of the basilar membrane is more pronounced, with four distinct changes readily identifiable. There is initially a gradual increase in area from the base for a distance of 7.4 mm,

FIG. 4. Photomicrographs of radial sections of (A) basal, (B) middle, and (C) apical coils of the organ of Corti showing (*i*) the division of the basilar membrane into the pars tecta (Pt) and the pars pectinata (Pp), using the outer pillar cell (short line in Fig. 4A) as the point of delineation between the two regions and (*ii*) the change in the thickened basilar membrane and the width of the basilar membrane (W). Arrows designate the limits used to measure the width of the basilar membrane. Scale bars = 100 μm.

followed by a sharp increase to a maximal area of about 58 × 10^{-4} mm^2 between 8.5 and 9.1 mm. There is then a decrease in area to about 38 × 10^{-4} mm^2 at about 12 mm and, finally, an increase to the apex. It is evident from Fig. 5 that the changes in the cross-sectional area of the basilar membrane are attributable to the pars pectinata, the larger part of the basilar membrane.

Changes in height (thickness) of the pars tecta and pars pectinata

Figure 6 illustrates the changes in the height (i.e., changes in the maximum thickness) of the cross-sectional area of the

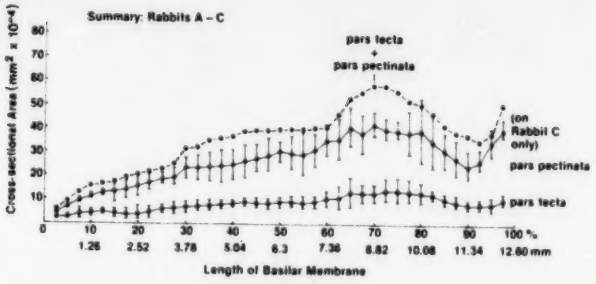

FIG. 5. An illustration of the changes in the cross-sectional areas of the pars tecta, the pars pectinata, and the basilar membrane (pars tecta and pars pectinata) along the length of the cochlea. See Fig. 4 for the reference points at which measurements were taken. The dots and vertical bars represent mean values and standard deviations, respectively. Note that the maximum overall cross-sectional area occurs at a distance between 8.5 and 9.1 mm from the basal end of the cochlea.

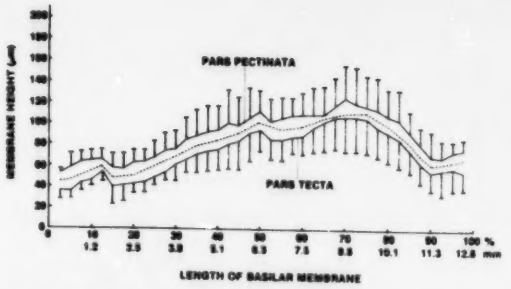

FIG. 6. Graphic depiction of the changes in height (i.e., the maximum thickness) of the pars tecta and pars pectinata of the basilar membrane. The dotted line represents the mean thickness of the basilar membrane; the vertical bars represent the standard deviations. Note (*i*) the similarity in the thickness and the cross-sectional area of the pars pectinata (see Fig. 5) and (*ii*) the differences between the height and cross-sectional area of the pars tecta (see Fig. 5).

pars tecta and the pars pectinata along the length of the cochlea. These curves show both similarities to and differences from those of the cross-sectional areas (see Fig. 5). There are gradual initial increases in height, with the maximal values in similar regions (near 9 mm). Then there are relatively rapid decreases preceding small increases near the apex. The curve of the height of the pars tecta differs from that of its cross-sectional area in that the curve of the area shows very little increase (see Fig. 5).

Ganglion cell density

An average total number of 26 700 bipolar ganglion cells was estimated within the spiral ganglion. The average cell soma axes were 27 μm × 22 μm. Figure 7 indicates the density of the bipolar ganglion cells along the length of the cochlea, i.e., the number of bipolar ganglion cells per unit cross-sectional area. Several distinguishing features are evident. First, there is an initial decrease in ganglion cell density from 2500 cells/mm^2 of cross section at the base to 1700 cells/mm^2 at 1.9 mm. The density then gradually increases to a plateau (about 2800 cells/mm^2) between 8.5 and 10.5 mm. Finally, there is a sharp drop in density as the apex is approached.

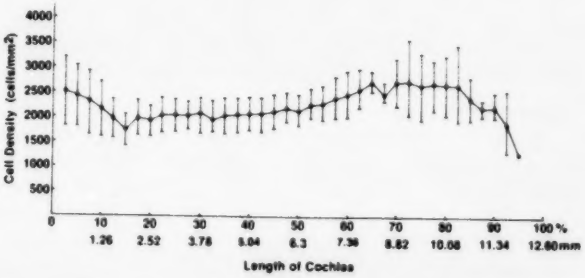

FIG. 7. The variation in the density of the bipolar ganglion cells along the length of the cochlea. The dots represent mean values and the vertical bars represent the standard deviations. Note that the curve decreases from the base for a distance of about 1.9 mm, increases gradually to a maximal value between 8.5 and 10.5 mm, and then decreases rapidly towards the apex.

Discussion

Comparative aspects of the changes in width of the basilar membrane

The variation in the width of the basilar membrane has been measured in several mammals: e.g., in the human (Guild 1927; Wever 1938), in the guinea pig (Fernandez 1952), in the cat (Cabezudo 1978), in the heteromyid rodent (Pye 1965; Webster and Webster 1977), in the house mouse (Ehret and Frankenreiter 1977), in some Cetacea (Wever *et al.* 1971, 1972), in some Microchiroptera (Pye 1966*a*, 1966*b*, 1967; Bruns 1976*a*; Henson 1978; Ramprashad *et al.* 1979), and in the two-toed sloth (Ramprashad *et al.* 1983). These studies have shown that in general, the basilar membrane increases in width between the base and the apex. The profiles of the curves for the cat, human, guinea pig, house mouse, heteromyid rodent, Cetacea, and two-toed sloth are all similar; however, the slope of the width to length of the cochlea differed markedly in each species (Cabezudo 1978; Ehret and Frankenreiter 1977; Webster and Webster 1977; Wever *et al.* 1971, 1972). In all the microchiropteran cochlea studied so far, the basilar membranes are unique in having a plateau of uniform width in the basal and middle coils of the cochlea (Bruns 1976*a*, 1976*b*; Henson 1978; Ramprashad *et al.* 1979). The curve of basilar membrane width versus distance in the rabbit (Fig. 3) is similar to the other species mentioned above and unlike the curve in Microchiroptera.

Comparative aspects of the changes in thickness of the basilar membrane

The curves showing changes in thickness of the pars tecta and pars pectinata in the rabbit do not differ markedly from those for the changes in cross-sectional area of the basilar membrane (cf. Figs. 5 and 6). Figure 6 shows that the curves of the thickness of the pars tecta and pars pectinata are similar, with mean maximal values of 106 and 124 μm at about 8.8 mm along the coil, respectively (i.e., in the middle coil). Figure 4 shows that the thickening of the pars tecta and pars pectinata in the rabbit results from enlargement of the fibrous layer. The thickening of the pars pectinata in the rabbit is similar to that reported in the cat (Cabezudo 1978), in Microchiroptera (Ikeda and Yokote 1939; Pye 1966*a*, 1966*b*, 1967; Henson 1970; Hall 1969; Ramprashad *et al.* 1978; Ramprashad 1979), in the house mouse (Ehret and Frankenreiter 1977), and in Heteromyidae (Pye 1965; Webster and Webster 1977). In Microchiroptera, the greatest thickening occurs within the basal coil. In the heteromyid rodents, it occurs in the upper second turn. In all these studies, the suggestion has been made that these thick-

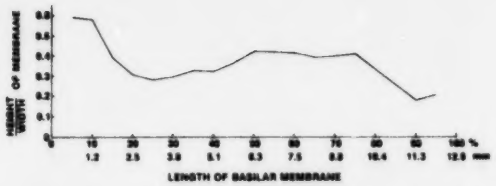

FIG. 8. The average change in the ratio of the thickness (height) of the basilar membrane to its width along the length of the rabbit cochlea. This ratio approximates the stiffness gradient along the basilar membrane. Note that there is a rapid decline in the stiffness gradient between 1.2 and 3.0 mm and that the stiffness gradient is relatively unchanged between 6.3 and 9.4 mm from the basal end.

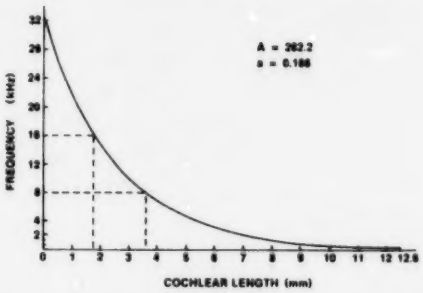

FIG. 9. The theoretical frequency response as mapped along the rabbit cochlea as determined from Greenwood's (1961) equation. Note that the frequencies of 8–16 kHz (broken lines) have maximal amplitudes of vibration in the region between 1.8 and 3.6 mm, a region in which the stiffness gradient of the basilar membrane is morphologically discontinuous as shown in Fig. 8.

enings may alter the manner in which the basilar membrane vibrates. If this is correct, then the dimensions recorded for the rabbit suggest that vibrational properties of its basilar membrane may differ in four distinct regions: (*i*) between 0 and 2.4 mm, (*ii*) between 2.4 and 6.3 mm, (*iii*) between 6.3 and 10.0 mm, and (*iv*) between 10 and 12.6 mm. It would be informative if it were possible to correlate audible frequencies associated with these areas along the basilar membrane.

Morphological considerations and hearing

The current understanding of mammalian hearing is based on the theory that travelling waves of particular frequencies maximally displace particular regions of the basilar membrane (Bekesy 1941, 1948, 1956). It follows then that the frequencies to which any mammal is maximally sensitive should coincide with particular regions of the basilar membrane and it seems reasonable to think that morphometric studies of the basilar membrane can provide information about the cochlear mechanics associated with mammalian hearing.

Previous morphometric studies on cochleae of some bats and the house mouse have suggested that a correlation exists between morphological discontinuities which occur on the basilar membrane and the most sensitive frequencies (Bruns 1976*a*, 1976*b*; Ehret and Frankenreiter 1977; Ramprashad *et al.* 1979). It has been suggested that these morphological discontinuities alter vibrating properties of the basilar membrane (Bruns 1976*b*; Ehret and Frankenreiter 1977). Bruns (1976*b*) has suggested that the ratio of basilar membrane thickness to its width, provides an approximation of the stiffness gradient of the basilar membrane. Figure 8 illustrates this approximation of the stiffness gradient for the rabbit. It shows that between 1.2 and 3.0 mm the gradient decreases, between 3.0 and 6.3 mm the gradient increases, from 6.3 to 9.4 mm the stiffness gradient is relatively uniform, and, finally from 9.4 to 12.0 mm the stiffness gradient decreases. It is of particular importance to note that the maximum density of bipolar ganglion cells also coincides with the region of the basilar membrane where the stiffness gradient was uniform.

Martin *et al.* (1980) determined audiograms for both pigmented and albino rabbits using the nictitating membrane response. The range of hearing is of the order of 0.3–32.0 kHz, with the most sensitive frequencies being between 8 and 16 kHz (at 10 dB relative to 0.0002 dyn/cm^2 (1 dyn = 10 μN)). Furthermore, the hearing ability of the pigmented rabbit is superior to that of the albino rabbit for low frequencies, in particular between 0.3 and 2.0 kHz.

The best-heard frequencies of the rabbit are from 8 to 16 kHz (Martin *et al.* 1980). It would be of particular interest to attempt to correlate where these frequencies are represented within the basilar membrane. Greenwood (1961) devised an equation which relates the position of maximum amplitude of vibration to the frequency,

$$f = A(10^{ax} - 1),$$

where f is the frequency in hertz, A and a are species-dependent constants, and x is the distance along the basilar membrane as measured from the helicotrema (apex) in units of "critical bands" (1 critical band ≈1 mm length of basilar membrane). For the rabbit, $A = 262.2$ and $a = 0.166$ (see Ramprashad *et al.* 1979 for further details). The curve in Fig. 9 shows the position of maximum amplitude of vibration for the frequencies 0.3–32 kHz along the basilar membrane according to Greenwood's (1961) equation. The maximum amplitude of vibration for the frequencies from 8 to 16 kHz occurs between 1.8 and 3.6 mm from the basal end, the region where the initial decrease of stiffness gradient occurs and the gradual increase starts (Fig. 8). In the rabbit, the maximum amplitude of vibration for the frequencies from 1 to 3 kHz occurs between 6.4 and 9.1 mm, the region of the basilar membrane where the stiffness gradient was relatively uniform (Fig. 8). Morphometric studies on the Microchiroptera and two-toes sloth cochleae have suggested that the best frequencies coincided within regions where the stiffness gradient was relatively uniform (Bruns 1976*a*, 1976*b*; Ramprashad *et al.* 1978; Ramprashad *et al.* 1979; Ramprashad *et al.* 1984). This correlation does not occur in the rabbit.

According to Greenwood's (1961) equation, therefore, the frequencies from 8 to 16 kHz, to which the rabbit ear is maximally sensitive, do not coincide within a region of uniform stiffness, but are found within a region of morphological discontinuity of the basilar membrane, namely a region in which there is a transition from a decreasing to an increasing stiffness gradient. However, the frequencies of 1–3 kHz do coincide within the region of the basilar membrane where the stiffness gradient is uniform.

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